

MODIFICATION OF PARENTAL BEHAVIOR DURING THE NESTING PERIOD IN THE COMMON BUZZARD (*Buteo buteo*)

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ABSTRACT.—The nesting behavior at five nests of common buzzards (*Buteo buteo*) was studied—two by video camera and three by direct observation. The objectives were to describe female behavior and to determine the proximate causes explaining why the female spent less time at the nest as the chicks grew. Before hatching, the female incubated almost constantly. The second period (days 0–8 after hatching) involved an active brooding pattern that occurred during feeding sessions. The third period (days 9–30) was characterized by a decrease in the variety of behavior performed by the female. Except for delivering prey, males were rarely involved in the direct care of the young. Furthermore, females did not deliver prey to the nest once they began to leave the young unbrooded for increasing periods of time. The female provided essentially all the care to the young after hatching. Her parental behavior was thwarted later by the increasing activity of the growing young, which is shown by a strong correlation between the time spent by the female at the nest and the activity of the young. This activity apparently led to the female's reluctance to stay at the nest in the presence of active young.

KEY WORDS: *behavior; Buteo buteo; incubation period; nestling period; parental care; prey delivery; reproduction.*

Cambio en la conducta parental durante el período de nidificación de *Buteo buteo*

RESUMEN.—Estudiamos la conducta de nidificación de *Buteo buteo* a través de registros de video y observaciones directas. Describimos la conducta de nidificación de la hembra y determinamos las causas proximas que podrían explicar la disminución progresiva del gasto en tiempo tanto en el nido como en la crianza de los pollos. Inicialmente, la hembra incubó casi constantemente. El segundo período (0–8 días después de la eclosión) involucró un activo patrón de ampolamiento que ocurrió durante las sesiones de alimentarias. El tercer período (9–30 días) se caracterizó por una disminución en la variedad de conductas desempeñadas por la hembra. Las hembras no entregaron presas en el nido hasta que comenzaron a dejar los juveniles por mayores períodos de tiempo. La hembra proveyó de todos los cuidados necesarios a los juveniles luego de la eclosión, pero más tarde, su conducta parental fue impedida por el aumento de actividad de los juveniles, lo que mostró una fuerte correlación entre la disminución del gasto de tiempo de las hembras en el nido y la actividad de los juveniles. Excepto por la provisión de presas, los machos, raramente se involucraron en el cuidado directo de los juveniles.

In most raptorial species the nest is attended by adults from 90–100% of the day during incubation and the first days after hatching (Rowe 1947, Rettig 1978, Stinson et al. 1988). In some species, the female becomes reluctant to leave the nest shortly before hatching, even at the approach of the male with food (Newton 1979). In those species in which males contribute to incubation, the female, usually dominant over the male (Carlier and Gallo 1989, Hubert and Carlier 1992), does not allow the male to perform incubation during the days immediately pre-

ceding and following hatching (Liversidge 1962, Wiley and Wiley 1981, Dewhurst et al. 1988, Village 1990).

Brooding behavior seems to wane after the nestlings have attained their second down plumage, as suggested in the gyrfalcon (*Falco rusticolus*; Jenkins 1978), or after becoming able to control their own body temperature, as suggested in the Eurasian kestrel (*Falco tinnunculus*; Village 1990). Once the female stops brooding, she spends most of her time in the vicinity of the nest (Wiley and Wiley 1981).

Nest attendance progressively reduces to feeding bouts and finally to food deliveries to the young. In most raptors, the transition between these phases is gradual and can occur on different schedules from nest to nest within the same species (Newton 1979). Although this nest attendance pattern has been described in several species, data are lacking for the common buzzard (*Buteo buteo*; Hubert 1990).

Most studies of the parental behavior in raptors implicitly assume that the adults behave in a way to satisfy the nestlings' needs (Jenkins 1978, Village 1990). For instance, adult hawks assist the thermoregulation of their nestlings by brooding or shading when chicks are small (Newton 1979), whereas the subsequent waning of female nest attendance is usually linked with the increasing nutritional needs of the young. In many species studied, the females do not deliver prey to the nest once they begin to leave the young unbrooded (Matray 1974, Jenkins 1978, Wiley and Wiley 1981). In the Eurasian kestrel, some females were never observed bringing prey to the nest during the nestling stage and attended the nest only during the first week following hatching (Village 1990). Why do females then leave the nest if not for hunting? Could other reasons explain the gradual waning of time spent by females at their nests?

Although natural selection would favor behavior that enhances nestling survival, the proximate factors motivating a bird to perform a particular behavior may be completely different from the evolutionary function. What are the proximate causes of the modification of the parental behavior? The aim of the paper is to test if buzzard females (1) leave the nest to satisfy the increasing nutritional needs of the young, or (2) leave the nest for another reason. One possible alternate explanation is that females leave the nest because of the increasing activity of the young, leading to an increasing avoidance of the young by the female.

METHODS

Area and Nest Sites. Nest-site characteristics have been described previously (Hubert 1992, 1993). We observed five pairs of buzzards nesting in the forest of Chizé (Deux-Sèvres, France) which is mainly composed of beech (*Fagus sylvatica*), oak (*Quercus pedunculata*) and pine (*Pinus sylvestris*). Nest trees were either beech, oak, or pine, and were located near pathways to facilitate a quiet and rapid approach by investigators. Nests were at a height of 14–20 m. Two nests were monitored by video camera and three by direct observation. Observations were made from 2 May to 10 June 1991.

Direct Observation. Three nests (nests C, D, and E) were monitored from ground level with a telescope (20–60×) and binoculars (8×) from observation sites 20–40 m from the nests for a total of 168 hr. The three nests were observed in succession in the morning for about 6 hr each per day. Nest C, containing one young, was observed directly from days 4–24 after hatching, then by video camera from days 28–45. Nest D, containing three young, was observed 5 d before to 10 d after hatching at which time the whole clutch suffered depredation. Nest E, containing three young at the beginning was observed from days 11–34 after hatching, but two young were killed by siblings (at age 14 and 32 d respectively) and the last one was found dead under the nest at age 37 d.

Video-recorded Nests. A video system, composed of a camera and a portable recorder powered by an automobile battery, was placed at two nests (A and B) each containing two eggs. The cameras (each protected by a plexiglas and wooden box and camouflaged by tree branches) were installed in trees 3–4 m above and 8–12 m from the nests. Each morning, at a fixed solar time, a new 4-hr tape was placed in the recorder. This created a small disturbance at the nest: the incubating female took off and returned 2–3 min later. This sampling regime was chosen because it appeared to be the time of maximum nesting activity in a preliminary study of full-day nest activity (Hubert 1990). Recording was done from 5 d before hatching until 18 d after hatching for nest A. The second young of nest A was killed by a predator in its 18th day of life (the first one died by sibling competition at 4 d). Then the video system was moved to nest C. Nest B was recorded from 13 d before to 32 d after hatching. Only one egg hatched, and this young was monitored until it was 32 d old. A total of 324 hr were filmed at the three nests (A, B, and C). Only the young of nest C was observed until flight, 43 days after hatching.

Behavioral Analyses. Video tapes were examined using a detailed ethogram describing movements, postures adopted, and the location of the behavior in the nest. The ethogram included 127 behaviors, but only the 34 acts occurring in behavioral sequences and appearing in correspondence analyses are described (Table 1). Videos were analyzed once by the same worker (C.H.), usually at normal speed, but some sequences (e.g., feeding bouts, nest arrivals, relationships between mates) were watched several times and slow motion was used. Data from direct observation nests were mainly used to ensure that recorded nests were consistent with other nests, but could not be as detailed as data from recorded nests.

Statistical Analyses. Behavioral sequences were statistically analyzed with SPAD.T software (described in Lebart et al. 1984, Morineau 1984, Lebart and Salem 1988), which can process a large number of diversified lexical data. Multifactorial data analyses were applied to the behavior of the females recorded at nests A and B (nest C was recorded too late in the nesting period to collect a large amount of data concerning the behavior of the female). Describing the behavior as a succession of acts (e.g., A, B, C, D, B, A, B) results in arbitrary breaks in a continuous activity. In order to regenerate natural groups of behavioral events with their transitions, series of repeated sequences of events were first identified (A–B, B–

Table 1. Non-exhaustive ethogram of female common buzzards at the nest. Only the acts involved in specific chains of behavioral sequences appearing on correspondence analyses are listed here (see methods).

AAC:	alarm attitude performed in the nest cup
AAR:	alarm attitude performed on the nest rim
ABR:	basic attitude of female landing at the nest (slanted, head in the neck, tail more or less spread)
AFC:	flattening in the nest cup while sitting on eggs
ASC:	scanning attitudes performed sitting in the nest cup
ASR:	scanning attitudes performed on the nest rim
ASS:	scanning attitudes performed standing up in the cup
BRC:	moving branches belonging to the rim from the center
F2:	tearing the prey into morsels
F3:	giving a food morsel to the young
F5:	morsel refused by young
F6:	ingesting morsel
F7:	picking up a fallen morsel
GUC:	getting completely up from the nest cup
GBC:	getting up backing off from the nest cup
GHC:	getting half up from the nest cup
H2C:	a series of two calls from the nest cup
H3C:	a series of three calls from the nest cup
INC:	incubation, sitting still on the eggs or young
PNC:	preening of the neck in the nest cup
PSC:	head-shake in the nest cup
PWC:	preening of the wing in the nest cup
ROC:	rocking movements (in order to place the clutch well in contact with her brood patch) while settling down or already sitting in the cup
RCC:	looking at the center (eggs or young) from the nest cup
RRC:	looking at the center (eggs or young) from the nest rim
SDC:	stepping down into the nest cup
THC:	turning herself in the nest cup
TEC:	this act refers to two different action patterns, the first one described by Gargett (1990) results in eggs turning: the female stretches her head forward and down to place her beak tip in front of the egg, slowly moving the egg toward her until it disappears beneath her breast feathers. The second one described by Ellis (1979) as 'bill-dig,' is a behavior oriented to the nest, where the beak and cere are buried in the nest cup. These actions were not always distinguishable and were combined as the same act, TEC.
WRR:	walking on the nest rim.

C, C-D, D-B, B-A, A-B-C, B-C-D, etc.). A threshold was applied to eliminate rare sequences and to retain the 150 more frequent sequences. Frequency tables were computed with the repeated sequences (A-B, B-C, C-D . . .) in lines and in rows for the observation days. The statistical association between lines and rows was then established (by calculations of the chi-square distance) and represented graphically by a correspondence analysis. Thus, a correspondence analysis illustrates the statistical relationships between sequences of acts and observation days, represented by a cluster of points. In two-dimensional space, the F1 factor is the main axis explaining most of the total variance. The F2 axis is the second most important factor in explaining the total variance, orthogonal to F1. On the graph, days with similar behavioral profiles are positioned closer. On the contrary, if days or sequences of acts are represented far away on one factor, it emphasizes an opposition between these days or these behavioral sequences for the concerned factor. Furthermore, evolution of female behavior from day to day is well described and characterized by the specific chains.

The most characteristic sequences ($N = 15$) were listed for each factor of the analysis. Rather than representing them on the graphs, transitions in groups of events were regenerated; e.g., the sequences A-B-C, C-B, and C-D were represented by the chain $A \rightarrow B \leftrightarrow C \rightarrow D$. Only the chains with the highest contribution to factors ($N = 15$) are represented in the figures.

Means are given with standard deviations. A Bravais-Pearson correlation test was used to calculate the link between the time spent by the female at the nest and the time during which the young was active (expressed in percent of observation time). The time of activity of the young was measured by the total sum of time spent in activities other than sleeping or being brooded.

RESULTS

Nest Attendance Schedule of Males and Females. Nest attendance of the females generally decreased 5–10 d after hatching (Fig. 1). The male, when allowed access to the nests (nests B and D), showed no regular pattern of attendance throughout the incubation period (maximum male attendance length observed was 1 hr, mean duration of stay during the incubation period was 6.5 min (SD = 3.6) at nest B and 3.0 min (SD = 1.0) at nest D, where males performed incubation). From 11–15 d after hatching, the females spent less than 50% of the observation time at the nest. About 25 d after hatching, females spent as little time at most nests as did males (except nest B).

After 15 d, the female of nest B was present at the nest more than the other females. Her nestling seemed slightly retarded compared to the average (at 31 d, it was still unable to eat alone and its feathers were less well developed than in other young of the same age). Because the young of nest A did not show

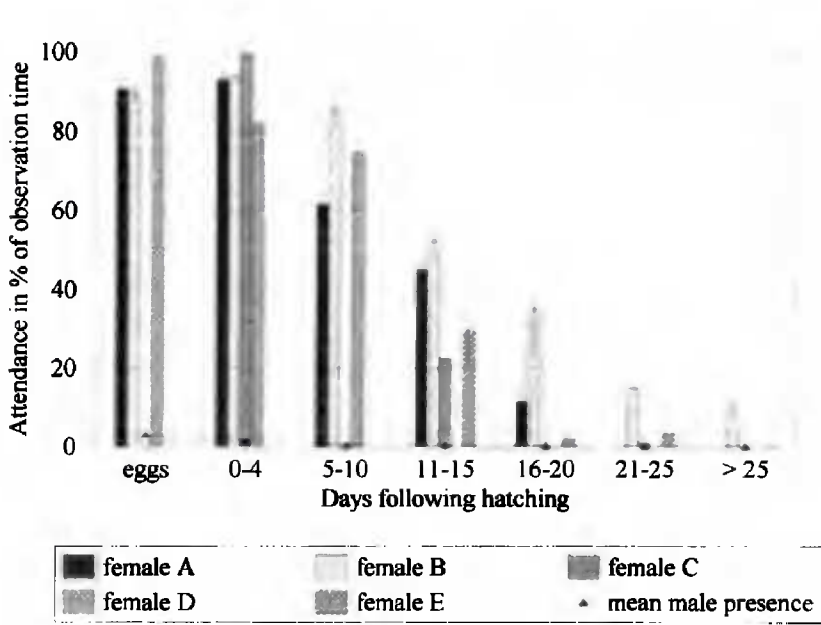


Figure 1. Common buzzard nest attendance in the forest of Chizé (France), observed from 2 May to 10 June 1991 (vertical lines are standard deviations).

an identical delayed growing pattern, this may not be due to an effect of the camera, but rather to different growing pattern between young.

Number of Prey Delivered by the Females According to the Age of the Young. The videotaped females (nests A and B) started to deliver some prey after the young were 16 d old (Fig. 2). But, their contribution in prey deliveries was equal to that of their mate at 25 or more days after hatching. Although females attended the nest for less than 50% of the observation time after 10 d, they did not deliver a substantial amount of prey until about 20 d. The number of prey delivered by adults at nests directly observed (nests C, D, and E) could not be estimated because the prey was usually not identifiable unless it was carried in the beak.

Analysis of the Behavior of the Female at Nest A. Correspondence analysis (Fig. 3) points out the relative similarity of days from (E-5)-Y8, opposed to days Y9-Y18 on the axis F1. There was no strong change in the behavioral profile of the female between 5 d before hatching and 8 d after. The behavior of the female incubating eggs or brooding a chick a few days old was about the same. From 5 d before to 8 d after hatching (Fig. 3), incubation/brooding (INC) was the primary behavioral activity, but a great number of acts were also involved. Chains of acts were long and involved a great diversity of acts. In Fig. 3, groups (E-1)-(E-5) and Y2-Y8 are distant on the second axis due to the emergence of feeding sessions.

The change in the female behavior occurred at 8-9 d after hatching. From Y9 to Y18, the female

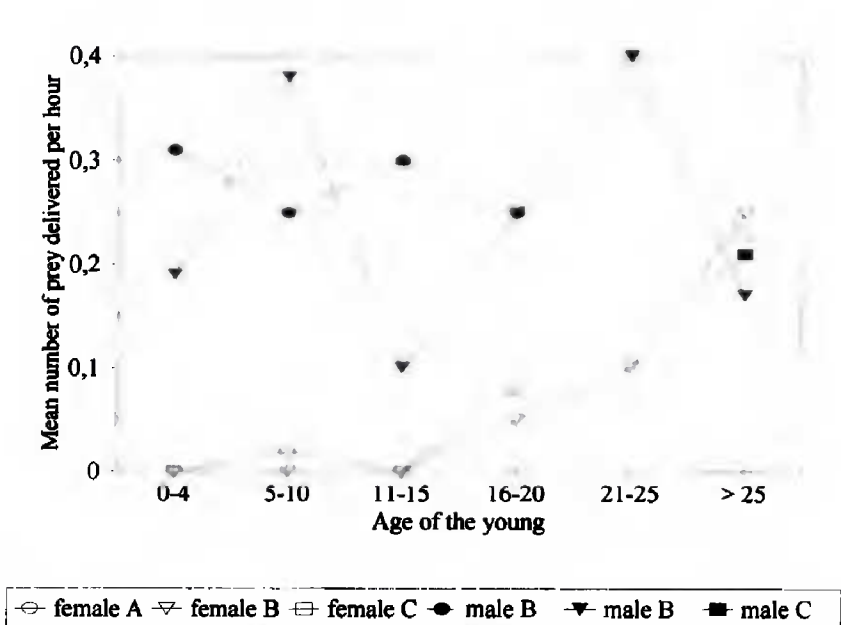


Figure 2. Number of prey items delivered to nest per hour by male and female common buzzards according to the age of the young (Forest of Chizé, 2 May to 10 June 1991).

behaved in a very homogeneous style (proximity of the points, Fig. 3). These days were typified by more effective feeding sessions. During Y9-Y18, females gave most of the food morsels to the young, whereas during Y2-Y8 the female ingested most of the torn morsels. Chains of acts were short and did not involve a great number of acts.

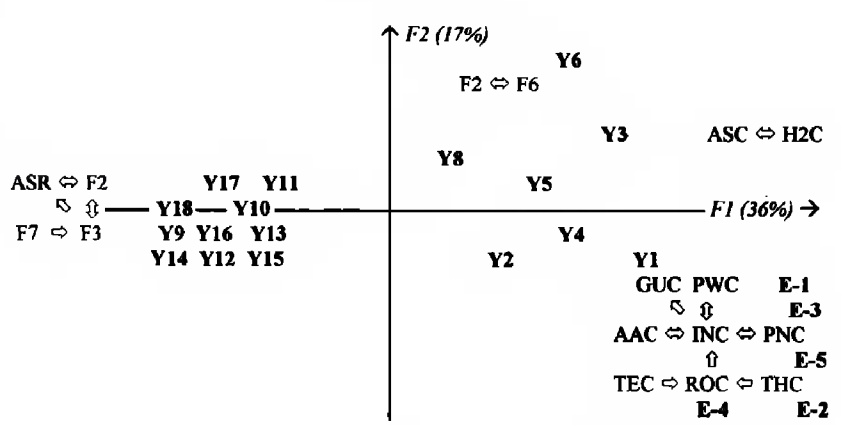


Figure 3. Correspondence analysis of the behavior of the female common buzzard at nest A according to the different observation days. See text for the explanation of chain construction and Table 1 for description of acts. Days (in bold characters) indicated the time preceding or following hatching; e.g., E-3 means 3 d before hatching (E = eggs), Y3 means 3 d after hatching (Y = young). Note the opposition on axis F1 between days (E-5)-Y8 and days Y9-Y18. The change in the female behavior occurred at 8-9 d after hatching. The group of days (E-5)-Y8 was characterized by incubation/brooding involving a great diversity of acts. The group of days Y9-Y17 was characterized by a reduction in the diversity of acts performed by the female (behavior reduced to feeding sequences).

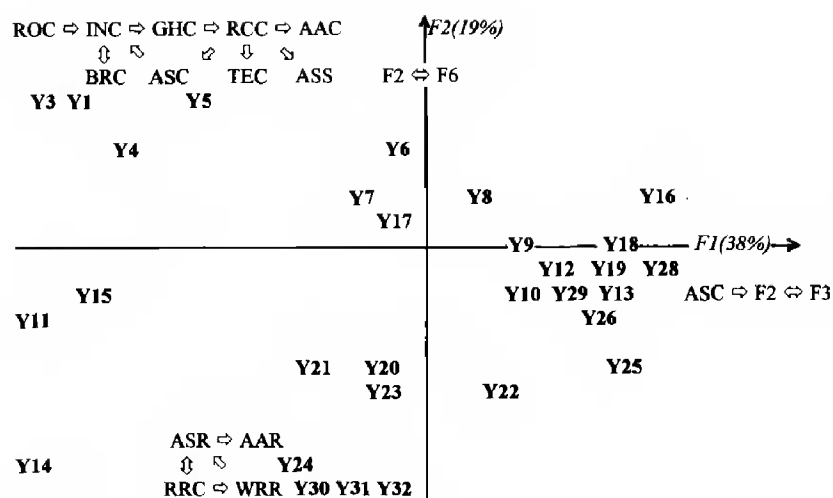


Figure 4. Correspondence analysis of the behavior of the female common buzzard at nest B after hatching. Acts belonging to a chain are described in Table 1. Days (in bold) indicated the time following hatching; e.g., Y6 means 6 d after hatching. Note the separation on axis F1 of days Y11, Y14, Y15 (days without feeding sessions at a stage where feeding occurred intensively), and separation of days Y1–Y8 from days Y9–Y32 (except Y16 and Y17, rainy days) on axis F2. Evolution of the female behavior occurred between the first days after hatching (characterized by a great diversity of acts), days Y9–Y25 (characterized by intense feeding sequences), and days Y30–Y32 (characterized by alarm attitudes on the nest rim).

Analysis of the Behavior of the Female at Nest B. Days Y1–Y8 were characterized by brooding behavior (Fig. 4), where the female performed a great number of diversified acts. Chains of behavioral acts were long and involved a great diversity of acts. Y16 and Y17 are included in this group because these

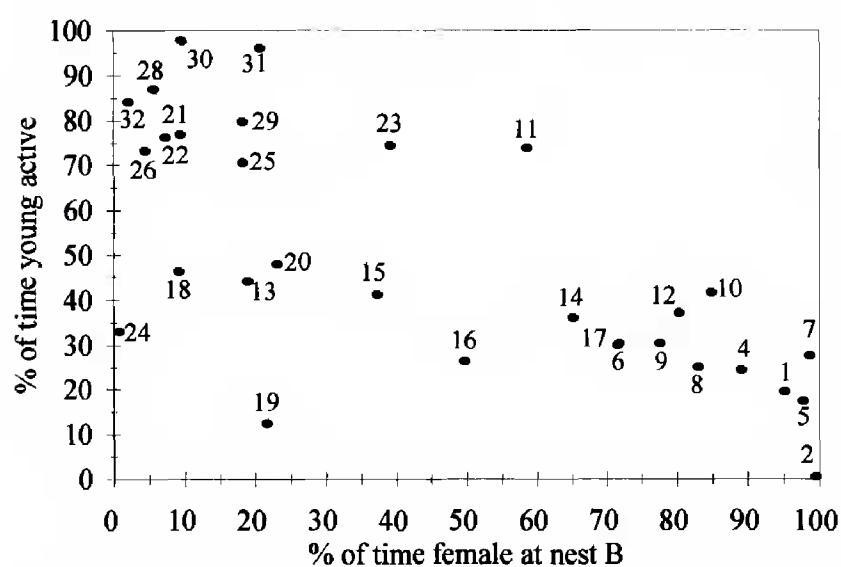


Figure 5. Correlation between time spent by the female common buzzard at the nest and the time of activity of the young (total of the time spent in activities other than sleeping or being brooded) recorded during 4-hr per day at the nest B ($r = -0.71$, $A = -0.92$, $N = 30$, $P < 0.01\%$). Numbers correspond to the age of the young.

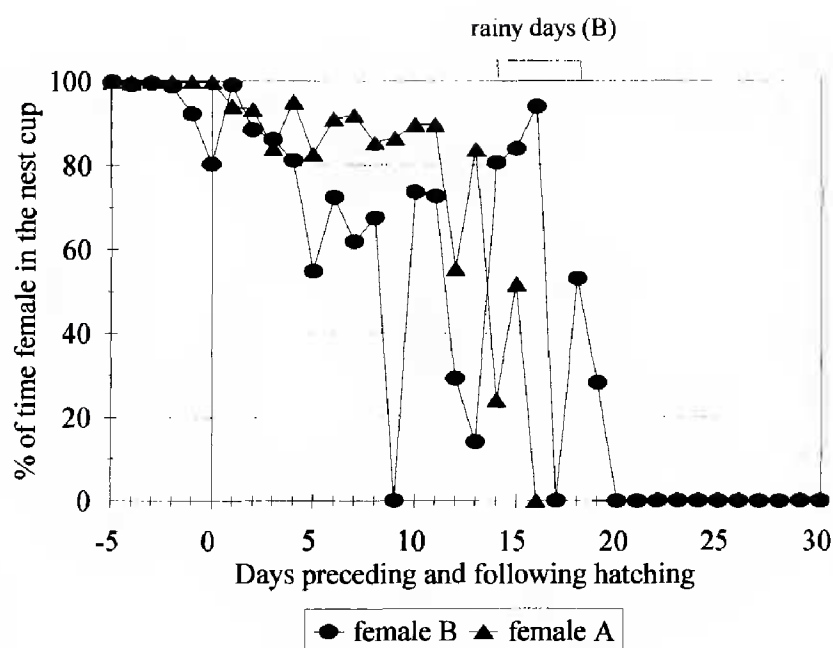


Figure 6. Time spent by female common buzzards in the nest cup versus the age of the young.

days were rainy (Y19 and Y20 also), and on both days the female behaved much the same as in the brooding period: she reached the nest as soon as it started to rain and stood over the young in the nest cup. Because of this behavior, these days are similar to days when the young were very small.

Y9–Y19 showed a decrease in the number and in the diversity of acts performed by the female at the nest (except during rainy days, Y16 and Y17) and intense feeding sessions (with F2–F3). The points are well clumped showing the homogeneity of the behavioral profiles on these days, if the young were fed (days Y11, Y14, and Y15 are widely separated from any group of points because these days were without feeding sessions at a stage where feeding occurred intensively).

As the young grew older, the female engaged more and more in many alarm and scanning attitudes (AAR, ASR), glances toward the nestling (RRC), and walking on the rim (WRR). During this period time at the nest was reduced to feeding sessions.

Observations at nests C and E revealed that after 30 d following hatching, the female, like the male, landed at the nest only to deliver prey. Her stays were reduced to a few seconds, the nestlings being able to eat alone. At this stage, the young begged aggressively to the arriving bird. Furthermore, the female did not exhibit her basic attitude (ABR) when landing at the nest, but exhibited the same alarm posture (AAR) as the arriving male.

Correlation Between the Time Spent by the Female at the Nest and the Time of Activity of

the Young for Nest B. The strong correlation (Fig. 5, $r = 0.71$, $r^2 = 0.5$, $P < 0.01\%$, $N = 30$) indicated that the activity of the young explained very largely the pattern of the female nest attendance. The more the young were active, the less the female was present at the nest. Note that the days are not well arranged in chronological order (Fig. 5).

Time Spent by Females A and B in the Nest Cup According to the Age of the Young. We observed that females attended the young until the nestlings were about 20 d old (Fig. 1). But the time spent by females A and B in the nest cup decreased after about 12 d (Fig. 6), whereas the time spent on the nest rim (and away from the nest) increased. After 15 d (except during rainy days in nest B where the female stood up in the nest cup), neither of the females ever entered the nest cup, and their stays at the nest were restricted to the nest rim.

DISCUSSION

Our results showed that as the young became older the variety of behavior performed by females at the nest was more and more limited. Furthermore, the area of the nest they occupied frequently was increasingly restricted. Thus, the performance of diversified behavior of females could be prevented by the presence of more and more active young in the nest. Furthermore, the fact that female nest attendance pattern was strongly correlated with the activity pattern of the young suggests that the female seemed to increasingly avoid contact with the active young. This avoidance behavior of the female seems to appear progressively (according to the correspondence analyses), but it is much more evident at a later stage of the nesting period. Indeed, after 25–30 d females behaved in the same way as males when landing at the nest. At this stage, not only the activity of the young increased, but the young were physically and behaviorally very different. Only the nestlings' head and neck were covered with down and the young adopted begging postures and mantled (wings and tail spread) over the prey.

Furthermore, this adult "avoidance hypothesis" seems to be consistent with findings of other authors. A reluctance of the adults to remain near their fledged young was noticed in some raptorial species (Jenkins 1978, Alonso et al. 1987, Gargett 1990). Nearly fledged golden eagles (*Aquila chrysaetos*) were even observed attacking their parents (Ellis 1979). In the black kite (*Milvus migrans*), before the first flights of the young, there was an increase in the amount

of time adults spent flying with prey in their talons before entering the nest (Bustamante and Hiraldo 1990). This could mean that the parent is reluctant to enter the nest with the aggressively begging young. Even though the literature shows that females have difficulty getting into the nest cup if it is full of large, aggressively begging young, our results show that females decreased brooding behavior before the size of the young for brooding became a factor (ca. 11–15 d). In the buzzard, it appears that the activity level of the young repels the parents rather than the performance of a particular behavior (such as begging). The "avoidance hypothesis" is consistent with the fact that the females did not leave the nest to hunt, because they did not deliver a substantial amount of prey before the young were over 25 days old.

During rainy days, the female was able to perform brooding: she landed at the nest and the 15–20-d-old young did not beg for food. She could stay in the nest cup with the young lying quietly under her until the rain ended. In other species, half-grown nestlings were also observed to be brooded during heavy rains or during windchills even though brooding in general had come to an end (Newton 1978, Jenkins 1978, Ellis 1979). Even if the ultimate explanation for this behavior is linked with the enhanced survival of offspring brooded during rain, the proximate cue for brooding in poor weather could be that the chicks, inactivity stimulates brooding. This hypothesis needs to be tested experimentally.

Our data suggest that the behavior of the female at the nest seems to be a compromise between her own motivation, environmental factors, and the behavior of the young. The brooding pattern of the female buzzard is freely performed until 9 d after hatching. Thereafter, the activity pattern of the female is characterized by a decreasing variety of acts on a decreasing area of the nest which is linked to the increasing activity of the young, and probably leading to the reluctance of the female to stay at the nest. Our conclusions cannot completely eliminate the possibility that the female is only responding to environmental conditions because of our restricted sample. Further investigations on larger samples are needed to shed light on the proximate causations and particularly on the motivational processes associated with parental behavior. For example, brood manipulations of nestlings of different age would allow to test if the modification of the female behavior is linked with the activity level of the young.

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